BIOENERGETICS OF A COVEY OF BOBWHITES[1]

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P URPORTEDLY many animals huddle or form roosting groups to conserve energy. This behavior decreases the surface area exposed to the environment and thus lessens dissipation of body heat. Despite frequent reference to it, this phenomenon seldom has been quantified. Kleiber and Winchester (1933) and Brenner (1965) quantified the efficiency of huddling in baby chicks and Starlings (*Sturnus vulgaris*), respectively. In other studies, mainly on small rodents (Retzlaff, 1939; Pearson, 1947, 1960; Sealander, 1952; Prychodko, 1958; Trojan and Wojciechowska, 1968) but also on avian species (Gerstell, 1939; Penney and Bailey, 1970), a metabolic advantage for huddling has been measured or such an advantage has been inferred from growth rates or survival times.

MATERIALS AND METHODS

Energy requirements were determined for Bobwhites (*Colinus virginianus*) under controlled conditions for a 10-hour photoperiod at seven temperature treatments from 5 to 35°C (at 5°C intervals). Equipment limitations prevented experiments at lower temperatures. Determinations were made for eight females, first individually confined and then kept as a single unit (covey). They were fed a balanced mash (prepared by the Department of Grain Science and Industry at Kansas State University): 20.5 percent protein, 2.7 percent fat, and 3.6 percent crude fiber; caloric value of 4.297 ± 0.004 kcal/g (mean ± SE).

The individual cages (48 × 25 × 13 cm) were made of polypropylene and had false wire bottoms and sliding tops (of ½-inch and ¼-inch mesh hardware cloth, respectively). Feed and water were provided ad libitum in glass feeders on the ends of the cages.

As a covey, the eight birds were kept in a wooden-frame cage (61 × 137 × 13 cm) eight times the floor area of an individual cage; the hardware cloth floor and top were of the same size as for the individual cage. The top of the covey cage was hinged in the middle to facilitate cage cleaning and bird removal. A sheet of water resistant, meat wrapping paper under the hardware cloth bottom caught excreta and spilled feed. Feed and water provided ad libitum, each in two dishes (7 cm high and 10 cm in diameter), reduced competition among birds.

A weighed amount of food (monitored for moisture and caloric value) was provided each day. At the end of 3 days, feed (uneaten and spilled) and excrement were collected, separated, and dried at 65°C to a constant weight. Birds, feed, and excrement were weighed to the nearest 0.1 g.

Feed or excrement was prepared for calorimetric analysis by grinding in a Wiley Model micro mill using a 20-mesh screen (0.51 mm openings). Samples were weighed to the nearest 0.1 mg prior to being analyzed in a Parr oxygen-bomb calorimeter. The mean of two determinations (differing by no more than ± 2.5 percent) was used for energy calculations.
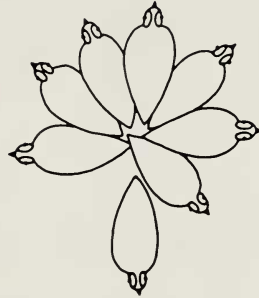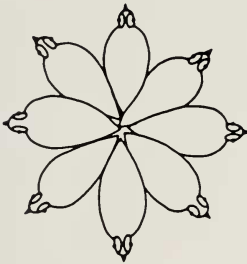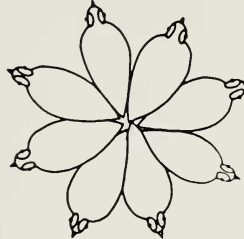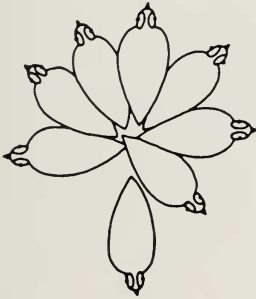
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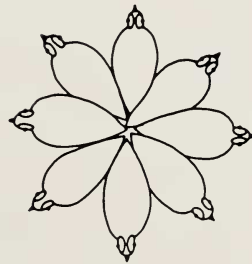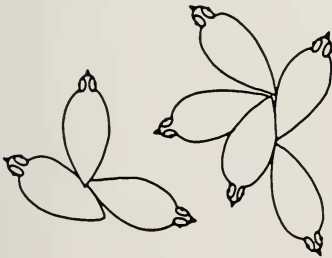of Observations**

5-15°C

20-30°C

35°C

Fig. 1. Types and relative frequencies of roosting formations observed as a function of ambient temperature for eight female quail at a 10-hour photoperiod.

Gross energy intake, excretory energy, and existence energy (see Cox, 1961 for definitions) were determined for each individual and for the covey. Stabilized weight, for existence energy, was defined as no more than ± 1 percent difference in body weight between the beginning and end of the 3-day period. Data for coveys are presented on a per-bird basis, and data on individual birds as means (for regressions) or deviations from
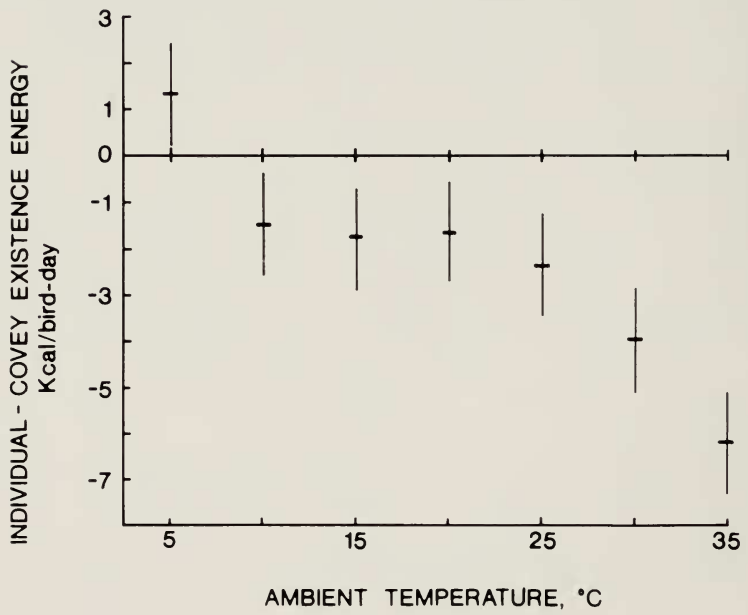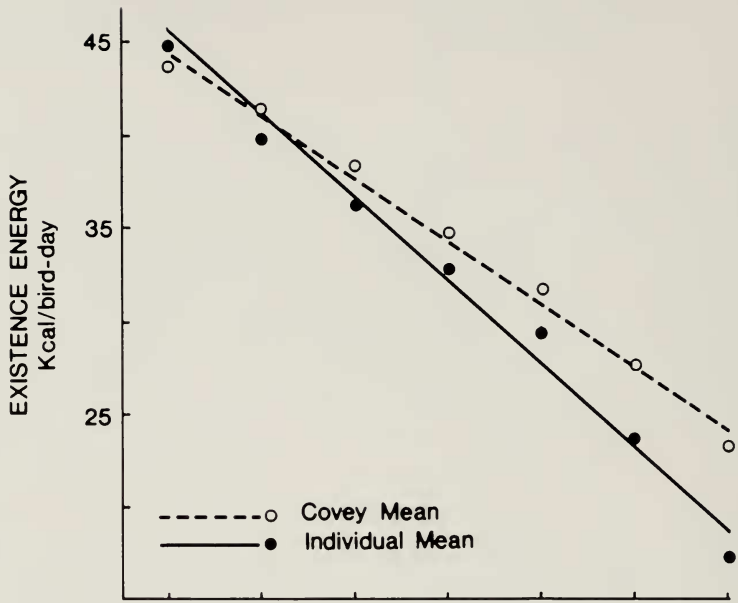
covey values (which permitted removing individual bird differences as a source of variation).

Covey Behavior.—The first attempt to form a covey was made with four quail of each sex. The birds existed amicably until the fourth day, at which time males became exceedingly aggressive toward each other. Since Stokes (1967) had found that female Bobwhites show little aggression in the absence of males, an all-female covey was attempted. The first day they were caged the birds formed their characteristic roosting disk and no overt aggressive behavior was observed throughout the experiment. Roosting formations tended to be more compact and compact formations more frequent at lower temperatures (Fig. 1).

Energetics.—Gross energy intake, excretory energy, and existence energy were inversely related to temperature for both covey and individuals. Regressions for each of those variables differed significantly between covey and individually caged birds ($P < 0.01$); no differences in intercepts were detected ($P > 0.10$) (see Fig. 2 for existence energy).

A two-way analysis of variance on differences between individually caged birds and the covey (per-bird basis) resulted in significant ($P < 0.01$) temperature differences for gross energy intake, existence energy, and coefficient of utilization (existence energy/gross energy intake, expressed in percent). In this analysis no temperature difference for excretory energy or body weight was detected. Mean body weights were at a minimum at 35°C, 171.8 and 172.9 g, for covey and individually caged birds, respectively; they were at a maximum at 20°C, averaging 191.1 and 189.7 g, respectively. Figure 2 shows the mean of differences between individuals and the covey for existence energy. Existence energy was greater for birds confined as individuals than for those in coveys at 5°C. At higher temperatures existence energy was greater for birds in coveys and at all temperatures the coefficient of utilization was greater for the covey than for individually caged birds. Coefficients of utilization did not differ significantly with temperature for individually caged birds ($\bar{x} = 76.22$); for birds in coveys they increased as temperatures increased (77.11 at 5°C to 81.45 at 35°C).

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FIG. 2. Existence energy of covey and individually caged Bobwhites at various temperatures. Upper half: simple regression for covey and individually caged quail. Covey: Y (kcal/bird-day) = 47.908 – 0.676 (°C), $r = -0.99$, $P < 0.01$. Individually caged: Y = 49.498 – 0.872 (°C), $r = -0.99$, $P < 0.01$. Lower half: mean ($\pm$ SE) of differences (individual – covey) in existence energy as a function of ambient temperature.

DISCUSSION

The aggressiveness of males was unexpected. In Kansas quail coveys do not start breaking up until late March or April (Robinson, 1957), when photoperiods are lengthening. Genelly (1955) found that most of the fighting in California Quail (*Lophortyx californicus*) took place between March and June. Stoddard (1932) associated aggressiveness in Bobwhites with the time of covey breakup. Possibly fighting occurred during my experiment (which began in February) as a result of the artificial conditions and confined space. Nestler et al. (1945), who interpreted pecking to be a manifestation of cannibalism and fighting in pen-reared Bobwhites, suggested pecking was an outlet for nervousness.

Though pecking about the head and neck was observed in the all-female covey, it was gentle and apparently caused no discomfort to the recipient. Stokes (1967) observed and interpreted such behavior in Bobwhites as preening. Stoddard (1932) and Rosene (1969) believed that quail acting this way were preening or removing lice.

In my experiment the behavior of the roosting birds appeared to substantiate huddling as an adaptive response to conserve energy. Roosting disks generally were more compact at low than at high temperatures, which verified laboratory and field observations of Stoddard (1932), Gerstell (1939), and Rosene (1969). But the quail occasionally formed tight roosting disks at temperatures as high as 30 or 35°C, indicating that temperature was not the only factor controlling this behavior.

Kleiber and Winchester (1933) showed that below the lower critical temperature (LCT), huddling chicks used less energy to maintain homeothermy than did individuals but that at or above the LCT, huddling had no metabolic advantage. My data for coveys seem to agree with that conclusion (Fig. 2). There was a metabolic advantage gained by huddling at 5°C, but at temperatures higher than that birds in coveys used more energy than did individuals. Since there was a leveling off, or plateau effect, of energetic variables (only existence energy is shown) from 10 to 20°C, apparently the LCT for Bobwhites occurred somewhere in that range. Brush (1965) found a LCT of 27.3°C for California Quail (which were summer acclimated) and Johnson (1968) found a LCT of 6.5°C for White-tailed Ptarmigan (*Lagopus leucurus*). A LCT of 10°C seems possible for Bobwhites in light of Kendeigh's (1969a) conclusion that the decrease in LCT in non-passerines was not great for various weight differences.

Although the leveling off of energetic variables could be a statistical artifact, a reasonable hypothesis might be that the LCT of Bobwhites in this experiment ranged from a minimum of 10°C to a maximum of 20°C, a range that could be attributed to change in temperature of acclimation and

a concomitant change in the feeding level. But I could not test my hypothesis by existence metabolism methods, from which no zone of thermal neutrality is evident (Kendeigh, 1969b). (The lack of a zone of thermal neutrality was verified by the high correlation of energetic variables with temperature with very little deviation from linearity.)

It was not clear why birds in coveys used more energy (directly related to temperatures $> 20°C$) than birds confined as individuals at warm temperatures or why they used feed more efficiently at all temperatures. Possibly birds in coveys had a higher existence metabolism because they ate more. And they ate more because of social facilitation, a common behavior in gallinaceous birds. (As one bird starts to feed, the others also may consume feed even though not hungry [Allee, 1958]). Penney and Bailey (1970) speculated that because of allelomimetic behavior ducks in groups of four consumed more feed than 2-bird groups. However, an increased level of feeding should result in increased weight or decreased use efficiency but my birds in coveys did not gain weight nor did their utilization efficiency decrease. An alternative explanation could be that my birds were more active when in a covey than when individually caged. Increased activity (accounting for increased efficiency in using calories) could have resulted from covey birds having a larger floor area to traverse, increased social interactions, mutual preening, and disturbances by other birds. It remains to be seen whether activity increases as temperatures increase.

How can we resolve the paradoxical situation of evolving and maintaining a social behavior that confers a metabolic disadvantage to covey existence during early fall and late spring? Occasionally cold temperatures (near and below freezing) do occur during those seasons, but why shouldn't covey behavior be manifested only when temperatures are cold? I believe that covey behavior is maintained, even though at a metabolic disadvantage, as a pre-adaptation for cold weather (when such behavior has survival values). Short-term cold spells (even overnight) would result in a metabolic advantage for huddling. The behavior, ultimately concerned with energy conservation (survival value), probably is under the proximate control of the photoperiod. It would be analogous, for example, to nesting and migration in birds.

Alternatively or concomitantly, huddling has a presumed adaptive advantage in regard to predation. Hamilton et al. (1967) proposed that massing Starlings maximized alertness to danger. The same could be true of Bobwhites, as the roosting disk is formed with heads directed outward. Rosene (1969) stated that a few birds in such a formation are always awake; that would further enhance alertness. Also, a covey would be less likely to be found by a predator by chance than would be birds uniformly dispersed

throughout a given area. Finally, the disruptive effect of a covey of birds flushing simultaneously could render a predator ineffective in picking out one bird to attack; and that would provide additional protection.

SUMMARY

Existence energy requirements of a covey of eight females were measured and compared with those of the same eight females individually confined.

The roosting formation generally was more compact at cold than at warm temperatures; huddling provided a metabolic advantage at 5°C but became energetically disadvantageous at higher temperatures. Occasionally tight roosting circles were observed at warm temperatures, when the behavior was seemingly metabolically disadvantageous.

Analyses of differences in energy requirements of individuals and covey resulted in a departure from linearity between 10 and 20°C, which presumably represented a shifting LCT (manifested by different temperatures of acclimation and a concomitant lower feeding level).

The adaptive significance of covey behavior when temperatures are warm enough to confer a seemingly metabolic disadvantage may be associated with proximate and ultimate factors. Ultimately the behavior is concerned with energy conservation, but the proximate control (which would be other than temperature) could be photoperiod. Roosting disks may also have an adaptive advantage in regard to predation.

LITERATURE CITED

ALLEE, W. C. 1958. The social life of animals. Beacon Press, Beacon Hill, Boston.

BRENNER, F. J. 1965. Metabolism and survival time of grouped Starlings at various temperatures. Wilson Bull., 77:388–395.

BRUSH, A. H. 1965. Energetics, temperature regulation and circulation in resting, active and defeathered California Quail, *Lophortyx californicus*. Comp. Biochem. Physiol., 15:399–421.

COX, G. W. 1961. The relation of energy requirements of tropical finches to distribution and migration. Ecology, 42:253–266.

GENELLY, R. E. 1955. Annual cycle in a population of California Quail. Condor, 57: 263–285.

GERSTELL, R. 1939. Certain mechanics of winter quail losses revealed by laboratory experimentation. Trans. N. Amer. Wildl. Conf., 4:462–467.

HAMILTON, W. J., III, W. M. GILBERT, F. H. HEPPNER, AND R. J. PLANCK. 1967. Starling roost dispersal and a hypothetical mechanism regulating rhythmical animal movement to and from dispersal centers. Ecology, 48:825–833.

Johnson, R. E. 1968. Temperature regulation in the White-tailed Ptarmigan, *Lagopus leucurus*. Comp. Biochem. Physiol., 24:1003–1014.

Kendeigh, S. C. 1969a. Tolerance of cold and Bergmann's Rule. Auk, 86:13–25.

Kendeigh, S. C. 1969b. Energy responses of birds to their thermal environment. Wilson Bull., 81:441–449.

Kleiber, M., and C. Winchester. 1933. Temperature regulation in baby chicks. Proc. Soc. Exp. Biol. Med., 31:158–159.

Nestler, R. B., D. R. Coburn, and H. W. Titus. 1945. Picking among pen-reared Bobwhite Quail. J. Wildl. Mgmt., 9:105–115.

Pearson, O. P. 1947. The rate of metabolism of some small mammals. Ecology, 28:127–145.

Pearson, O. P. 1960. The oxygen consumption and bioenergetics of harvest mice. Physiol. Zool., 33:152–160.

Penney, J. G., and E. D. Bailey. 1970. Comparison of the energy requirements of fledgling Black Ducks and American Coots. J. Wildl. Mgmt., 34:105–114.

Prychodko, W. 1958. Effect of aggregation of laboratory mice (*Mus musculus*) on food intake at different temperatures. Ecology, 39:500–503.

Retzlaff, E. G. 1939. Studies in mass physiology: growth rate with the white mouse. J. Exp. Zool., 81:343–356.

Robinson, T. S. 1957. The ecology of Bobwhites in south-central Kansas. Univ. Kansas Mus. Nat. Hist. and Biol. Surv. Kansas, Misc. Publ. No. 15.

Rosene, W. 1969. The Bobwhite Quail, its life and management. Rutgers Univ. Press, New Brunswick, New Jersey.

Sealander, J. A., Jr. 1952. The relationship of nest protection and huddling to survival of *Peromyscus* at low temperature. Ecology, 33:63–71.

Stoddard, H. L. 1932. The Bobwhite Quail; its habits, preservation and increase. Charles Scribner's Sons, New York.

Stokes, A. W. 1967. Behavior of the Bobwhite, *Colinus virginianus*. Auk, 84:1–33.

Trojan, P., and B. Wojceichowska. 1968. The influence of darkness on the oxygen consumption of the nesting European common vole *Microtis arvalis* (Pall). Bull. Acad. pol. Sci., Ser. sci. biol., 16:111–112.

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